THE FLORISTIC DISJUNCTIONS BETWEEN THE "MONTE" IN ARGENTINA AND THE "SONORAN DESERT" IN MEXICO AND THE UNITED STATES[1]

OTTO T. SOLBRIG[2]

One of the best known but most puzzling disjunctions is that between the temperate regions of South America and the temperate regions of North America. It is puzzling because it involves a large number of floristic elements, and because it is evident from the geological data available that the two regions have never been closer to each other than they are today (Dietz, 1961).

Raven (1963, 1971) has addressed himself to this problem and has very accurately pointed out that we are dealing with more than one type of disjunction. There is the disjunction involving elements that grow in the cold regions of South and North America; the disjunctions involving plants that grow in areas with a Mediterranean type of climate in both continents; the disjunctions between areas with a mesic hydric and temperature regimes; and finally the disjunctions between the so-called "desert areas." In his reviews, Raven presents evidence that indicates that these disjunctions are relatively recent and that they probably have arisen almost exclusively by long-range dispersal.

However, Raven did not discuss in detail the disjunction involving the desert areas. This is the best known one (Bray, 1898, 1900; Campbell, 1944) and probably the most controversial. It also involves the largest percentage of the flora. In this paper I want to present data that lead me to believe that we are dealing with patterns of distribution that have been established over a long period of time and that no one single explanation can encompass them all. In order to clarify the discussion, only plants that grow in the phytogeographical province of the "Monte" in Argentina and the "Sonoran Desert" in Mexico and the southwestern United States will be discussed.

DESCRIPTION OF THE TWO REGIONS

The Monte and the Sonoran Desert are remarkably alike in their physical characteristics (Hauman, 1947; Morello, 1958; Shreve, 1951; Shreve & Wiggins, 1964; Solbrig, 1972). Basically they are ecological semideserts with mild winters and hot summers, rainfall that rarely exceeds 300 mm, and negative evapotranspiration throughout most of the year. The rainfall regime varies within both areas. Each region has areas of winter rainfall, winter and summer rainfall, and only summer rainfall.

Physiognomically both areas can be described as xerophytic scrubs with a predominance of perennial shrubs. These show a series of adaptations to a deficient water economy such as small leaves, sunken stomata, thick cuticles with

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[2] Department of Biology and Gray Herbarium, Harvard University, Cambridge, Massachusetts 02138.

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waxy and resinous exudates, etc. In addition to the shrubs, other conspicuous elements are succulents, particularly Cactaceae, Bromeliaceae, Agavaceae, and Fouquieraceae. A third element is the annual flora, which grows in conjunction with the rains and consequently, both winter and summer annuals can be identified.

In areas that span such latitudinal and altitudinal ranges as the Monte and the Sonoran Desert, by necessity variations in all kinds of physical and biological parameters will be encountered. There will be truly "desert" elements as well as riparian elements that because of their ability to tap underground water are able to escape to a degree the limitations that lack of water impose on plant growth. This should be borne in mind when the disjunctions are discussed in detail. It also applies to the density of the vegetation and total coverture that one is likely to find. Although basically both regions are characterized by less than 100% coverture, this is not always so, particularly in those areas where more humidity is locally available for one reason or another.

The Floristic Similarities

The flora of the Sonoran Desert has been recently studied by Shreve and Wiggins (1964). Although they give no exact figures, a rough estimate is that it is formed by approximately 3,000 species. No comparable work exists for the Monte, the closest being Morello's (1958) study of the vegetation, which cites 307 species in a list that does not wont to be complete. The exact figure is probably closer to 3,000. Of this total of roughly 5,000 species growing in both areas, only some 100 to 150 are disjunct or pairs of closely related species, roughly 2 per cent. The number of genera in common is much higher, the regions sharing approximately 50 of the roughly 500 genera growing in both areas, that is approximately 10 per cent. On a purely numerical basis the common elements are not very great. What is impressive is that among the elements that are shared by both areas are some of the most important species of both areas.

First in importance is the creosote bush, gobernadora or jarilla, *Larrea divaricata*, the most important perennial shrub in the Sonoran Desert and in the Monte. In both areas *Larrea divaricata* occupies hundreds of square miles with an abundance of 90% or more. In the Monte two other species of *Larrea*, *L. cuneifolia* and *L. nitida*, often replace *L. divaricata*, but the latter is still the most important species.

The second most important element with a disjunct distribution is the genus *Prosopis*, sect. *Algarrobia*, the "mesquite" and "algarrobos." Although there are no common species between South and North America, *P. chilensis* from South America and *P. juliflora* from North America are very closely related and were considered conspecific at one time. These trees are the principal riparian element in both the Monte, where they have speciated extensively, and in the North American deserts.

A number of other floristically abundant shrubs and trees also show disjunct distributions or have pairs of closely related species at the northern and southern sites. Among them are the genus *Celtis* in the family Ulmaceae, represented in South America by *C. spinosa* and in North America by *C. pallida* and *C. laevigata*;

the genus *Condalia* in the Rhamnaceae, represented in the Sonoran Desert by *Condalia lascioides* and *C. spathulata* and in the Monte by *C. microphylla*; also in the Rhamnaceae the genus *Ziziphus*, represented by *Z. mistol* in the Monte and by *Z. sonoriensis* in the Sonoran Desert; in the Leguminosae we find among others *Caesalpinia gillesii* with a disjunct distribution and the genus *Cercidium* with closely related species at both sites; and finally in the Capparaceae, the species *Atamisquea emarginata* is a very conspicuous element of the flora of both the Monte and the Sonoran Desert. All these species are important elements of their respective vegetations, being widespread and abundant.

Members of the family Cactaceae are very conspicuous elements of the flora of the Monte and the Sonoran Desert. Although several genera are shared by both regions, notably *Opuntia* and *Cereus*, no close relationship at the specific level is known that can not be traced to a recent introduction by man (such as the "choya" cactus *Opuntia fulgida*, introduced into Argentina in historic times). There is however a great ecological and morphological similarity, notably among the giant "saguaro" and "organ" type cacti.

In addition to the species and genera mentioned, a great number of species and genera which occupy a much less conspicuous role in the vegetation have species in common, or pairs of closely related species. Although some of these genera are woody, most notably some of the compositae, the majority are herbaceous.

THE DISTRIBUTIONAL PATTERNS

There are three main explanations that can be brought forward to explain the floristic similarities between North and South America. They are as follows: that the disjunction has arisen as a result: (1) of long-distance dispersal; (2) of a once continuous distribution; or (3) of parallel convergent evolution. All three explanations have been brought forward, and there are reasons to believe that all three are applicable in some instances.

Long-range dispersal. It will never be possible to say conclusively that a certain pattern of distribution is due to long-range dispersal. However, with a judicious use of Okam's razor, circumstantial evidence may point to long range dispersal as the most likely explanation.

For the Monte-Sonoran disjunction, long-range dispersal is obviously the simplest explanation if the dispersal agent is not considered. However, it becomes much more difficult to see how long-range dispersal can be effected if the possible dispersal agents are considered. Wind as a dispersal agent can be discarded from the onset. The flow of air, both at the surface and in the upper atmosphere, at every time of the year is such that it is impossible for seeds to be carried from one area to the other by wind across the equator. Neither is there any evidence that the flow of air masses was different in the past. We can therefore safely discard wind as an agent of long-range dispersal between the Monte and the Sonoran Desert.

This leaves only animals as possible agents of dispersal. Obviously more knowledge is needed, and particularly experimental work to determine the effectiveness of birds as agents of dispersal. Species of birds are known that fly from the United States to Argentina in their migration flights. None of these inter-

continental migrators are birds of the desert areas, however. To consider them as agents of dispersal it must be hypothesized that either regularly or occasionally they stop at the periphery or the center of the areas under consideration. A further complication is the well-known behavior trait of migrating birds of flying with an empty gut. Seeds still could be carried on feet or plumage. In any case, birds as agents of migration can not be ruled out, but neither are they a very likely source.

What makes long-range dispersal attractive as an explanation in certain cases is the pattern of distribution of certain species. Axelrod (1950) has shown that the vegetation of the North American desert areas has two main sources: one is the so-called Arcto-Tertiary element, a northern, cold-temperate source; the other is the so-called Madro-Tertiary element from a warm-tropical source. Raven (1971) has pointed out that because of its geographical situation the southern hemisphere has not produced an equivalent of the Arcto-Tertiary flora. Although this interpretation is open to discussion and more work on the fossil floras of the southern hemisphere is needed to shed light on this point, it is undoubtedly true that most of the elements of the flora of the dry temperate areas of South America have a tropical origin as Raven (1971) has pointed out. This is also true of the Monte, where Leguminosae, Zygophyllaceae, Rhamnaceae, Cactaceae, etc. are the dominant elements.

If this line of reasoning is accepted, then it is tempting to assume that disjunct species belonging to northern genera not represented in the tropics have been dispersed by long-range dispersal. Particularly some grasses such as *Bephlaridagne benthammianae*, *Andropogon saccharoides*, *Stipa speciosa*; Compositae such as *Verbesina encelioides*, *Encelia farinosa*, etc. that possess small seeds, are herbaceous, either annual or short-lived perennials, might have dispersed this way. In some cases such as *Leptochloa uniflora* the pattern of dispersal involves a series of steps across the equator.

In summary, although it is hard to envision how exactly seeds are carried across the equator, certain patterns of distribution are easiest to explain assuming long-range dispersal in recent times.

Continuous distribution across the tropics. The greatest intellectual block in accepting this explanation is the existence of a tropical belt between the Monte and the Sonoran Desert. It is well known that plants are good dispersers across physical gaps such as water barriers or mountain ranges, but poor dispersers across climatic barriers.

Although this is an undeniable fact, it might not be as formidable a consideration as it appears. Plants are capable of tolerating a greater set of environmental conditions than those to which they are exposed, as witnessed by the variety of ambients where species can grow under cultivation. What usually happens is that although plants are able to grow, they are not able to compete under the warmer climatic regimes.

At present, desert conditions exist scattered across the tropics of South America, and what evidence exists points to the existence of such areas also in the past (Harrington, 1962; Vuilleumier, 1971). Such dry areas exist mostly in the lee of mountains in the western parts of the continent. Competition in such areas is

mostly for water, and it is possible that plants from more mesic, but dry areas, such as the Monte and the Sonoran Desert, could have used these areas as stepping stones in moving from North to South or vice versa.

Indirect evidence for such an explanation is found in the present distribution of certain characteristic shrubs and trees. *Cercidium* is a genus of seven species. Two of these are found in the Monte and adjacent areas; four in the Sonoran and Chihuahuan Deserts; and the last, *C. praecox*, has an almost continuous distribution from Mexico to Peru, through the Antilles. *Cercidium praecox* is so closely related to the Monte species that it is considered conspecific by some botanists, and although the North American species are more distinct, it appears very likely that the genus spread from North America to South America or vice versa through the intervening dry tropical areas.

The genus *Bulnesia* in the family Zygophyllaceae is formed by seven species. It is obviously of tropical origin and speciated in the Chaco and adjacent areas of South America. The species *Bulnesia retama* is a conspicuous element of the flora of the Monte. This is the most xeric species of the genus. The distribution of *Bulnesia retama* is of interest because it extends from Argentina to Venezuela, again hopping through the dry areas. Although *Bulnesia* is not found in the Sonoran Desert, it conceivably could get there in the future if populations can become established in the Antilles. Also in the Zygophyllaceae, the distribution of *Larrea divaricata* is of interest. This dominant element of the Monte and Sonoran Desert has a few intermediate stations in Bolivia and Peru. It is tempting to postulate that the species once had a broader range of distribution in the tropical areas.

In brief, there are patterns of distribution particularly among the shrubs and trees that point to a more continuous distribution across the islands of xeric climate in the American tropics, and this explanation at least for cases such as *Cercidium* can not be ruled out.

Convergent evolution. The final alternative explanation for the disjunct distribution says that we are not dealing with a disjunction at all, but with a case of convergent evolution. The proponents of this hypothesis (Barbour, 1969) state that those elements that are tropical in nature might have produced, under the selection of the similar climates of the desert region of the Monte and the Sonoran Desert, similar or identical types through convergence. The major problem with this hypothesis is to find an independent criterion to discriminate between it and the other two. Nevertheless, the distribution of the genus *Prosopis* is suggestive of the validity of the idea of convergence, at least in some cases.

Prosopis is one of the most primitive genera of the Mimiosoid-Legumes. Species of *Prosopis* grow in the Old World (Asia Minor and East Africa) as well as in the Americas, where they are found from the southern United States to northern Argentina. The distribution suggests an early Tertiary or even Cretaceous origin for the genus, since at that time Africa and South America were joined together. It also suggests a tropical origin. This idea is reinforced by the distribution of the sections, with the primitive section *Algarrobia* being both tropical and subtropical in distribution, while all the other more specialized American sections are either found in the mountains or temperate regions.

If we look at the various species of *Prosopis*, sect. *Algarrobia*, we find that the less specialized species are found in the more mesic areas both in the tropics and in the temperate zones, while the more specialized species are found in the Monte and the Sonoran Desert. This is accompanied by the development of similar morphological specializations in leaf structure and habit. The convergence is, however, not so great as to put any doubt on the separate origin of the North and South American desert species. However, presumably the process could proceed to the point where the species may become identical morphologically. If this were accompanied by the extinction of the parental species, the resulting distributional pattern would be suggestive of long-range dispersal.

Summary and Conclusions

The American tropics are flanked by areas with semidesert climate. These xeric belts possess some floristic elements in common. Since they are separated by some 6,000 miles across tropical climate, this presents a formidable problem. Three hypotheses to explain those disjunctions have been proposed: (1) long-range dispersal; (2) continuous distribution across the tropics in the past; and (3) convergent evolution from tropical ancestors. There is circumstantial evidence in favor of the possible correctness of each of the three hypotheses in special cases. What is now needed is careful, detailed work with the species involved in order to obtain more insights into their genetics, cytology, chemistry, and ecological relationships.

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